

Current Biology

Early Permian synapsid impressions illuminate the origin of epidermal scales and aggregation behavior

Highlights

- *Bromackerichnus* n. igen. is the earliest resting trace of synapsids
- *Bromackerichnus* includes the earliest epidermal scales of synapsids
- Eight tetrapod groups had epidermal scales during the early Permian global warming
- *Bromackerichnus* associations suggest group behavior of sphenacodonts

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In brief

Marchetti et al. describe *Bromackerichnus*, the first definite body impression of early synapsids and, more specifically, sphenacodontids. *Bromackerichnus* includes the earliest fossil evidence of epidermal scales in synapsids, long before the acquisition of hair. Marchetti et al. evidence how the acquisition of epidermal scales might be related to the early Permian aridization. *Bromackerichnus* is a resting trace found in associations co-occurring with swimming and sliding traces, evidencing gathering of sphenacodonts in or near pools.



Report

Early Permian synapsid impressions illuminate the origin of epidermal scales and aggregation behavior

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SUMMARY

Fossil evidence of skin structure^{1,2} and group behavior^{3,4} in the stem group of mammals, the early synapsids, is sparse and restricted to a few occurrences. We describe here exceptional resting trace fossils, *Bromackerichnus requiescens* n. igen. n. isp., from the early Permian Tambach Formation at the Bromacker locality, Thuringia, Germany.⁵ They are the only definite early synapsid—and, more specifically, spenacodontid—full-body impressions. They include skin impressions of the limbs, trunk, and tail that show epidermal scales and are associated with *Dimetropus leisnerianus* footprints. Through a morphological comparison with modern taxa,⁶ we demonstrate for the first time the unequivocal occurrence of epidermal scales in early synapsids. A review of the early amniote and stem amniote trace and body fossil skin record highlights that this constitutes the oldest occurrence of epidermal scales in synapsids, long before the acquisition of hair.⁷ Moreover, we find the first fossil occurrence of epidermal scales in eight different tetrapod groups during the early Permian. This implies an earlier common origin of epidermal scales. The higher chance of preservation and spreading in the early Permian was probably due to a structural reinforcement of the scales as an adaptation to global warming and aridization⁸ at the end of the Late Paleozoic Ice Age. Moreover, spenacodontid resting, swimming, and locomotion traces of multiple individuals of different sizes co-occur on the same bedding planes, in a relatively small area. This is interpreted as the earliest documented aggregation behavior in spenacodontid synapsids that gathered in and around small ponds.

RESULTS

Systematic paleontology

Bromackerichnus requiescens n. igen. n. isp. Figures 1 and 2 and Table S1.

Etymology

From the Bromacker locality, Latin *ichnus*, trace, and Latin *requiescens*, resting.

Material

Holotype MNG 1821 (holotype), MNG 1765 and MNG 14944 (paratypes), MNG 1822, MNG 1828, MNG 1983, MNG 1987, and MNG 13490. Fine-grained sandstones with traces preserved as natural casts.

Type locality

Bromacker locality, Thuringia, Germany. Tambach Sandstone Member, Tambach Formation (Cisuralian, Sakmarian), Thuringian Forest Basin (Figure S1).

Diagnosis

Resting trace of a tetrapod (with a trunk about 8–16 cm wide). The trunk impression is craniocaudally short and transversally broad compared with the putative neotridian resting trace *Hermundurichnus*,⁹ which is instead characterized by a thin trunk impression. No medial ridges or lines are observed, different from *Temnocorpichnus*¹⁰ and *Hermundurichnus*. Semi-lunate lateral skin flap impressions as those observed in *Hermundurichnus* are not present. The forelimb impressions are at a low angle compared with the trunk impression, different from *Temnocorpichnus*, in which the forelimbs are perpendicular to the trunk impression. Limb impressions are relatively smaller, compared with the body, than in *Temnocorpichnus*. The relatively thin (about 1/6 of the trunk width) and straight tail impression differs from *Temnocorpichnus*, which shows a wider (about 1/3 of the trunk width) and shorter tail impression. The occurrence of scale impressions on trunk, limbs, and tail differs from *Temnocorpichnus*, which does not show scaly skin impression. The rhomboidal to rectangular scale impressions of the trunk are aligned in a grid of slightly caudolaterally bent transversal and longitudinal rows

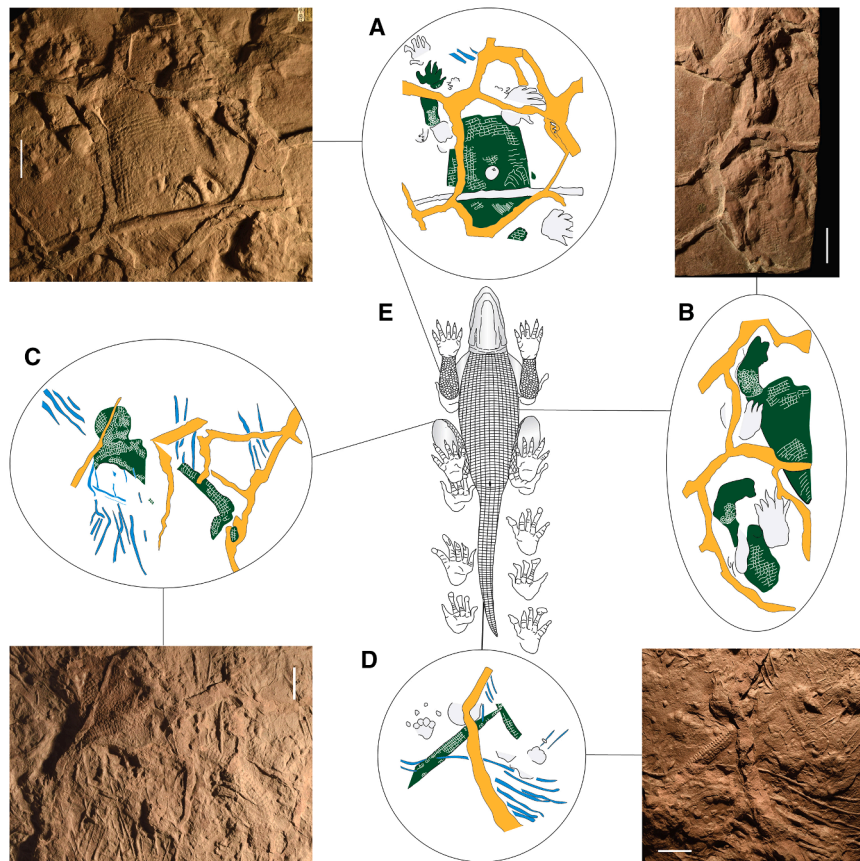


Figure 1. Spnenadontid body impression, *Bromackerichnus requiescens* n. igen. n. isp.

(A–D) Photos with oblique light and interpretive drawings. All specimens in convex hyporelief; scale bars, 5 cm. Body impressions in green, swimming traces in blue, footprints and other trace fossils in gray, and mud cracks in orange. (A) MNG 1821, holotype. Trunk and right forelimb impressions with scalation pattern, right manus and left pes impressions (*Dimetropus leisnerianus*) with scale grooves. (B) MNG 1765, paratype. Two body impressions side by side, showing trunk impressions and right forelimbs with scalation pattern and indistinct manus impressions. (C) and (D) MNG 14944, paratype. (C) Two body impressions. The one on the left of the photo includes lower trunk, pelvic and proximal tail, and right hindlimb impressions with scalation pattern. The one on the right of the photo includes tail and left proximal hindlimb impressions with scalation pattern. (D) Two tail impressions with scalation pattern, crossing each other at right angle.

(E) Reconstruction of the producer of *Bromackerichnus requiescens* n. igen. n. isp. with scalation pattern and hypothetical trackway leading to the resting position, bottom view. The gray areas are not impressed. Artwork by Sophie König.

that differ from *Hermundurichnus*, in which these scale impressions are aligned in rows with a more irregular pattern. The forelimb ends in a pentadactyl manus impression and the body trace is associated with a pes impression, which are both assignable to *Dimetropus leisnerianus*, different from *Temnocorpichnus*, in which the forelimb ends in a tetradactyl manus impression assignable to *Batrachichnus salamandroides*.

Description

Body impression of a tetrapod with a relatively short (16–24 cm) and wide (8–16 cm) trunk (Figures 1A and 1B). The whole trunk impression is characterized by rhomboidal to rectangular scales, each about 4 or 5 mm long and wide, arranged in a grid of transversal and longitudinal (craniocaudal) rows. The transversal rows are slightly bent caudolaterally. Scales on the lateral parts of the trunk are slightly more prominent; this is observable in the scale profiles (Figures 2E and 2G; sections 4 and 5). No medial ridges are observed. No head and neck impressions are preserved. Forelimb impressions are relatively short and thick compared with the body (Figures 1A and 1B), with the orientation of the lower arms diverging at a low angle from the trunk (-19° to 11°). Forelimb width is 3 cm, length 5–6 cm. The distal forelimb impression is covered by oblique-trending rows of hexagonal scale impressions, each about 2 or 3 mm in diameter, which sometimes follow a regular arrangement. These scales are smaller and more prominent than those on the trunk. They show a profile with higher relief (Figure 2D; sections 2 and 3). Only the proximal part of the hindlimb

impression is preserved and is about 6 cm wide, at a relatively high angle to the trunk (44° – 57° , Figure 1C). The proximal hindlimb impression is covered by rectangular (limb side facing the tail) to hexagonal scales (ventral side of the limb) about 5 mm long and wide, perpendicular to the limb direction. These rows are slightly curved, following the curvature of the limb, and show scales overlapping on the ventral side of the limb. These scales show an asymmetric profile, having sides of different lengths and inclinations (Figure 2I; section 7). The connection between tail and hindlimb is distinctly curved, and the side shows regular rows of rectangular scales. Tail impressions are straight, long, and thin (Figures 1C and 1D). The maximum tail length is about 26 cm, and tail width is about 3 cm. The tail impression is covered by longitudinal rows of rectangular and prominent scales. These scales show a profile with high relief and clear hinge regions (Figure 2K; sections 8 and 9).

Associated traces

The right forelimb of the resting trace of MNG 1821 ends in a pentadactyl, ectaxonic (i.e., with relatively longer lateral digits) manus impression about 5 cm long and 6 cm wide (Figure 1A). Digit IV is the longest, digit V is about as long as digit II (Table S1). Digit imprints end in sharp claw impressions and show rectangular scales as wide as the digits, about 5 mm in length. An associated incomplete left pes imprint is 5 cm long and 6 cm wide (Figure 1A). It is ectaxonic; digit IV is the longest, digit V is shorter than digit II (Table S1). Digit II ends in a bifurcated impression. Digits show clear rectangular scales as wide as the digits and about 5 mm in length. Complete autopodia impressions, ectaxonic,



Figure 2. Scale impressions of spheonacodontids

Body impressions of *Bromackerichnus requiescens* n. igen. n. isp. associated with *Dimetropus leisnerianus* footprints.

(A and B) MNG 1821. (A) Incomplete step cycle with left pes-manus couple and left pes associated with a tail impression with rectangular scalation pattern. (B) Left manus impression with rectangular and prominent scales.

(C and D) MNG 1765. Forelimb hexagonal scale impressions.

(E–G) MNG 1821. Trunk scale impressions, overview (F), rhomboidal scales (E) and rectangular scales (G).

(H and I) Hindlimb scale impressions. Hexagonal and overlapping (upper left of the photo) and rectangular (lower right of the photo).

(J and K) MNG 14944. Tail scale impressions, rectangular and prominent. All specimens in convex hyporelief; scale bars, 5 cm. 1–9, vertical sections of photogrammetric 3D models of the specimens. Note the asymmetric scale profile in 7 and the strongly concave scale profiles with clear hinge regions in 1, 8, and 9.

right forelimb almost parallel to the body and the manus imprint turned medially. The body impressions do not seem to overlap.

Remarks

We introduce a new ichnotaxon, *Bromackerichnus requiescens* n. igen. n. isp. for the described body impressions (Figure 1). They are unequivocally associated with footprints that we assign to *Dimetropus leisnerianus* because they are ectaxonic, ending with claw traces, with laterally elongated palm/sole impres-

sions and digits more deeply impressed at their base and at their end¹¹ (Figures 1A, 2A, and 2B). This material represents body impressions of tetrapods, based on the morphology and arrangement of the different body parts, including trunk, limb, and tail regions. Also, the regular rows of polygons are identified as scale impressions because their morphology and arrangement are consistent, regular, and repeated and found only on the body impressions (Figures 2, S2, and S3). This differs from structures such as interference ripples (e.g., “*Hauboldichnus*,” see the discussion in Haubold¹²) and from microbially induced sedimentary structures (Figure S4), sometimes mistaken for scale impressions.¹³ For the first time, we propose an ichnotaxonomic assignment of the body impressions from the Tambach Formation (including a detailed description of the body impressions and scales) and demonstrate their anatomical connection with *D. leisnerianus* tracks, all of which were not attempted in previous work.^{12,14} The body impressions described herein differ from other early tetrapod amphibian impressions, such as *Hermundurichnus*,⁹ *Temnocorpicinus*,¹⁰ and other unnamed amphibian^{15,16} and reptile¹⁷ body impressions, because of the

Aggregation traces

MNG 14944 yields at least four tail impressions (Figures 1C and 1D). The two tail impressions on the left of the slab are directed about 90° compared with each other, and they seem to overlap, which would suggest that the animals left them at a slightly different time. The two tail impressions and partial hindlimbs on the right of the slab are facing opposite directions and do not overlap.

Specimen MNG 1765 (Figure 1B) displays two body impressions aligned side by side (although one is more distal compared with the other) in an almost identical pose. This includes a part of the trunk with visible scalation pattern, a right forelimb with scales, and a manus imprint. Both body impressions show the

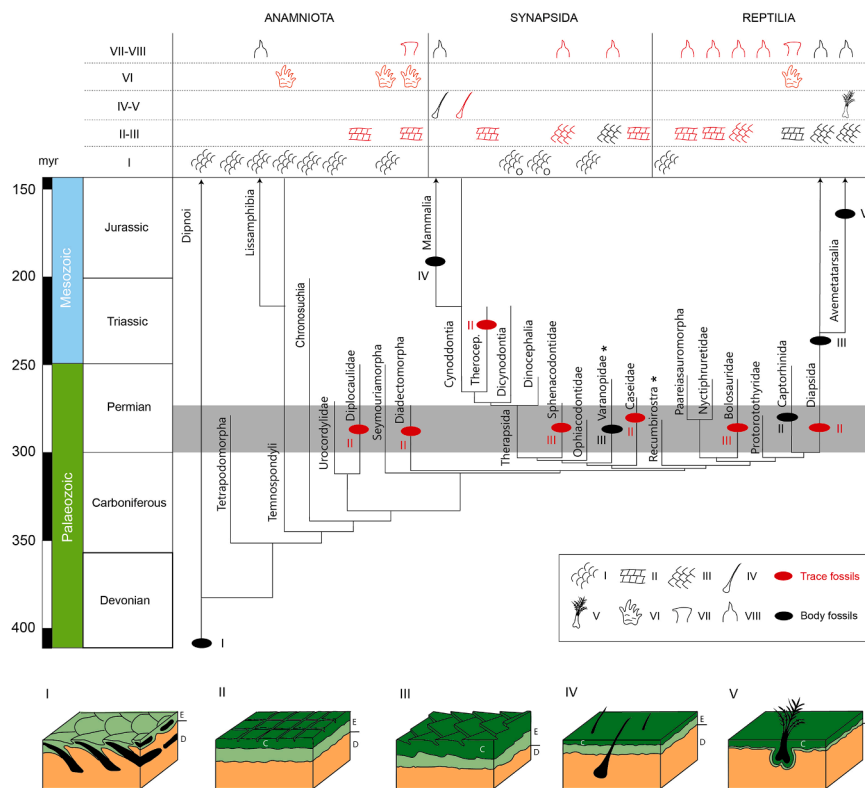


Figure 3. Early evolution of ventral scalation pattern and autopodia skin folds

Cladogram from Mann et al.²⁵ and Ruta et al.²⁶ Asterisks indicate clades with debated phylogenetic position.²² I–VIII, vertebrate integumentary and claw structures; I, dermal scales and other dermal ossifications (o); II, epidermal scales; III, thickened epidermal scales/overlapping scales; IV, hair; V, feathers; VI, skin folds on autopodia; VII, claw sheaths; VIII, claws; D, dermal layer; E, epidermal layer; C, stratum corneum. Ellipses represent the first occurrence of the feature in a specific cladogram branch. Note the high occurrences of new epidermal structures in the early Permian (gray area).

maximal composite length of *Bromackerichnus* n. igen. (about 50 cm, trunk length of MNG 1821 and tail length of MNG 14944, Table S1); nevertheless, some specimens (e.g., MNG 1765) seem smaller.

DISCUSSION

Early tetrapod skin evolution

Epidermal scales (Figures 2, 3, S2, and S3) with a polygonal shape forming rows in a grid-like or alternating arrangement are found only in reptiles⁶ (including birds²⁰) among extant tetrapods. *Bromackerichnus* n. igen. shows rows of prominent polygonal scales with a definite hinge region (Figure 2), this is in agreement with the development of epidermal scales in early synapsids. As such, the earliest occurrences of epidermal scales in synapsids are from the early Permian trace fossil record, and specifically from the Sakmarian of Germany (Tambach Formation, this study) and the Artinskian of France (Rabejac Formation, this study), attributed to sphenacodontids and caseids, respectively. This type of integument is also known from early Permian varanopids, from the Sakmarian of Germany (Leukersdorf Formation²¹); however, varanopids are currently considered either synapsids or reptiles.²² Impressions of epidermal scales are visible in Middle Triassic footprints, potentially made by therocephalians.²³ Epidermal scales may therefore have had a long stratigraphic range in non-mammalian synapsids (Cisuralian–Middle Triassic) and potentially occurred in at least three different families. Crown-group mammals appeared in the Late Triassic and may have acquired endothermy (and thus hair) no later than the Jurassic.²⁴ Whether the co-occurrence of scaly skin and hairy appendages was common in early Mesozoic mammal relatives or whether transitional skin structures occurred is not clear from the fossil record.

The first occurrences of epidermal scales in the reptile body fossil record are in the early Permian, specifically captorhinids from the Artinskian of Oklahoma (Richard Spur fissure fills)²⁷ and in the trace fossil record of parareptile and diapsid traces, both from the Asselian of Germany (Goldlauter Formation).^{12,17} The earliest potential record of these structures in anamniotes is in the early Permian trace fossil record, from the Asselian of

overall morphology of the trunk, limbs, scalation patterns, and associated tracks (Figures 1 and 2).

Tracemakers

Dimetropus leisnerianus tracks have been attributed to pelycosaur-grade synapsids,¹¹ with the exception of varanopids. Few non-varanopid synapsid genera are time-equivalent with the stratigraphic range of the Bromacker site (Figure S1), and even less have a completely known postcranial skeleton and autopodia. At the Bromacker locality, skeletal remains of non-varanopid synapsids have been found, including the sphenacodontid *Dimetrodon teutonius* and the caseid *Martensius bromackerensis*.^{18,19} Both show a large tarsus and a digital arcade in the digits (Figure S5), both features consistent with the proximal-lateral elongate sole impression and the paw-like impressions of *Dimetropus leisnerianus*. We compared trace fossil measurements for *Bromackerichnus* n. igen. and the associated *Dimetropus leisnerianus* with skeletal measurements of a selection of potential non-varanopid synapsid producers of the same age of the Bromacker locality (STAR Methods; Tables S1 and S2). Results indicate that *Martensius* has a noteworthy longer manual digit V compared with the *Dimetropus leisnerianus* footprints. *Palaeohatteria* has a gleno-acetabular length too short and *Ophiacodon* shows a pes/manus length ratio too high compared with the trace fossils. Because *Edaphosaurus* and *Sphenacodon* do not occur at the Bromacker locality (and *Ophiacodon* not even in Europe), it is reasonable to assume that *Bromackerichnus* n. igen. and the associated *Dimetropus leisnerianus* were produced by *Dimetrodon teutonius* or similarly proportioned yet unknown synapsids. The calculated maximal snout-vent distance of *D. teutonius* (55 cm, Berman et al.¹⁸) is comparable with the

Germany (Rotterode Formation) and Poland (Ślupiec Formation), attributed to the groups Nectridea⁹ and Diadectomorpha,²⁸ respectively.

Rows of overlapping epidermal scales (Figures 2, 3, S2, and S3) are characterized by a zigzag-like surface due to the sigmoidal folding of the epidermis. In modern animals, these structures are found only in the highly cornified skin of reptiles.⁶ Among synapsids, a similar structure is observed in spheonacodontid trace fossils from the Sakmarian of Germany (Tambach Formation, this study). In the fossil record of reptiles, morphological indications for overlapping scales are observed in Triassic diapsid skeletons and tracks.²⁹ The earliest occurrence is in an early Permian trace fossil of parareptiles, from the Asselian of Germany (Goldlauter Formation^{11,17}). In the amniote skeletal record, one of the earliest occurrences is in early Permian varanopids, from the Sakmarian of Germany (Leukersdorf Formation²¹).

The overall similarity of epidermal scalation shared by distinct groups of early amniotes is noteworthy, as well as the fact that its earliest fossil occurrence in six different amniote and two anamniote groups (or 7 amniote and 1 anamniote groups, depending on the phylogenetic placement of diadectomorpha³⁰) was in the early Permian (Figure 3). The occurrence of epidermal scales in the last common ancestor of amniotes is supported by trace fossils attributed to amniote stem groups with likely impressions of epidermal skin featuring scalation.^{9,28} Because similar epidermal scales are observed in both modern reptiles and early amniotes, including prominent and overlapping epidermal scales in both early reptiles²⁷ and synapsids (this study), we assume that this similarity is due to a common origin of these skin structures, probably in the Carboniferous. Subsequently, the evolution of epidermal scales in reptiles and synapsids may have followed a similar convergent adaptation. In fact, studies on extant reptilian epidermal scales show that they have different derived mechanisms of cornification.^{31,32} The spreading of epidermal scales to eight different groups and the acquisition of more reinforced epidermal structures in reptiles and synapsids points to an adaptation to dryer paleoenvironments during the early Permian global warming⁸ which required integuments to become more suitable at retaining body water.

Early synapsid group behavior

The combined study of exceptionally preserved trace fossils and depositional environments of the Bromacker locality provides unique information on the paleoecology of spheonacodontids.

Some specimens display multiple resting traces assigned to *Bromackerichnus* n. igen. Such concentration of body impressions of the same producer in a small area would suggest an aggregation behavior. In fact, we interpret the resting traces on MNG 14944 as body impressions of four different individuals (Figure 4B) because they have very different orientation and no transitions between one trace and the other is visible, as it is in documented cases of multiple body traces created by the same individual.¹⁶ Moreover, we interpret the resting traces on MNG 1765 (Figure 4C) as two individuals resting side by side because they do not seem to overlap each other, have a similar orientation, and there is no sign of transition between each other.

The close relation between *Bromackerichnus* n. igen. producers and a muddy, shallow water paleoenvironment is accounted for by the presence of numerous swimming traces

found alongside *Dimetropus* tracks and *Bromackerichnus* n. igen. resting traces (Table S3; Figure 4B). They show the typical morphology and arrangement of swimming traces, with sets of thin, long, and parallel traces.¹¹ Moreover, they differ from drag marks linked to locomotion¹¹ as they do not begin and end with a *Dimetropus* track. In MNG 14944, some of the swimming traces cut the resting traces, suggesting that the resting traces may have been produced underwater. Swimming and sliding traces are preserved in depressed areas in MNG 13490 (Figures 4E and 4F). Moreover, MNG 1823 (Figure 4A) shows parallel trackways of *Dimetropus leisnerianus*, whose preservation changes significantly along their course, suggesting that the animals were moving out of a water pool, consistent with the occurrence of microbial mats and the larger mud crack size, indicating a thicker mud layer.⁵ This evidence would support the hypothesis of possible resting behavior of the *Dimetropus leisnerianus* producers in shallow water (Figure 4G).

The Tambach Formation at the Bromacker locality is characterized by marked wet and dry seasonality.^{5,33} In periods of drought, the spheonacodontid trackmakers of *Bromackerichnus* n. igen. could have gathered in mud ponds. The dorsal sail in early synapsids has been hypothesized to play a thermoregulatory role,³⁴ but although the dorsal sail function is still up for debate,³⁵ mud-bathing could have also helped to keep a cooler temperature. This behavior can be seen in semi-aquatic reptiles nowadays, such as crocodilians in periods of drought.³⁶ Gathering in extant reptiles such as crocodilians can also be for reproductive purposes³⁶ or collaborative hunting.³⁷ Further in agreement with the lifestyle of extant crocodiles, collaborative hunting may primarily have happened at night, as indicated by the supposed nocturnality of spheonacodontids.³⁸ Although the causes are difficult to discern, the described resting traces are strongly suggestive of an early evolution of spheonacodontid aggregation behavior in water pools (Figure 4H).

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to, and will be fulfilled by, the lead contact Dr. Lorenzo Marchetti (lorenzo.marchetti@mf.berlin).

Materials availability

The authors declare that the specimens MNG, which are the focus of this study, are housed at the Friedenstiftung Gotha, Germany.

Data and code availability

- The studied material is available at publicly accessible institutions. Institutional abbreviations: CM, Canadian Museum of Nature, Ottawa, Ontario, Canada; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MB, Museum für Naturkunde Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNC, Museum für Naturkunde Chemnitz, Germany; MNG, Friedenstiftung Gotha, Germany; NHMW, Naturhistorisches Museum Wien, Austria; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SS, Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie, Freiberg, Saxony, Germany; UGKU, Umweltmuseum Geoskop, Thallichtenberg, Germany; UR, University "La Sapienza" of Rome, Italy.
- All the data used in this study are included in Tables S1–S3.
- All raw computed tomography (CT) scan data and parameters are made available on MorphoSource (MorphoSource ID: 000720516).
- This paper does not report original code.

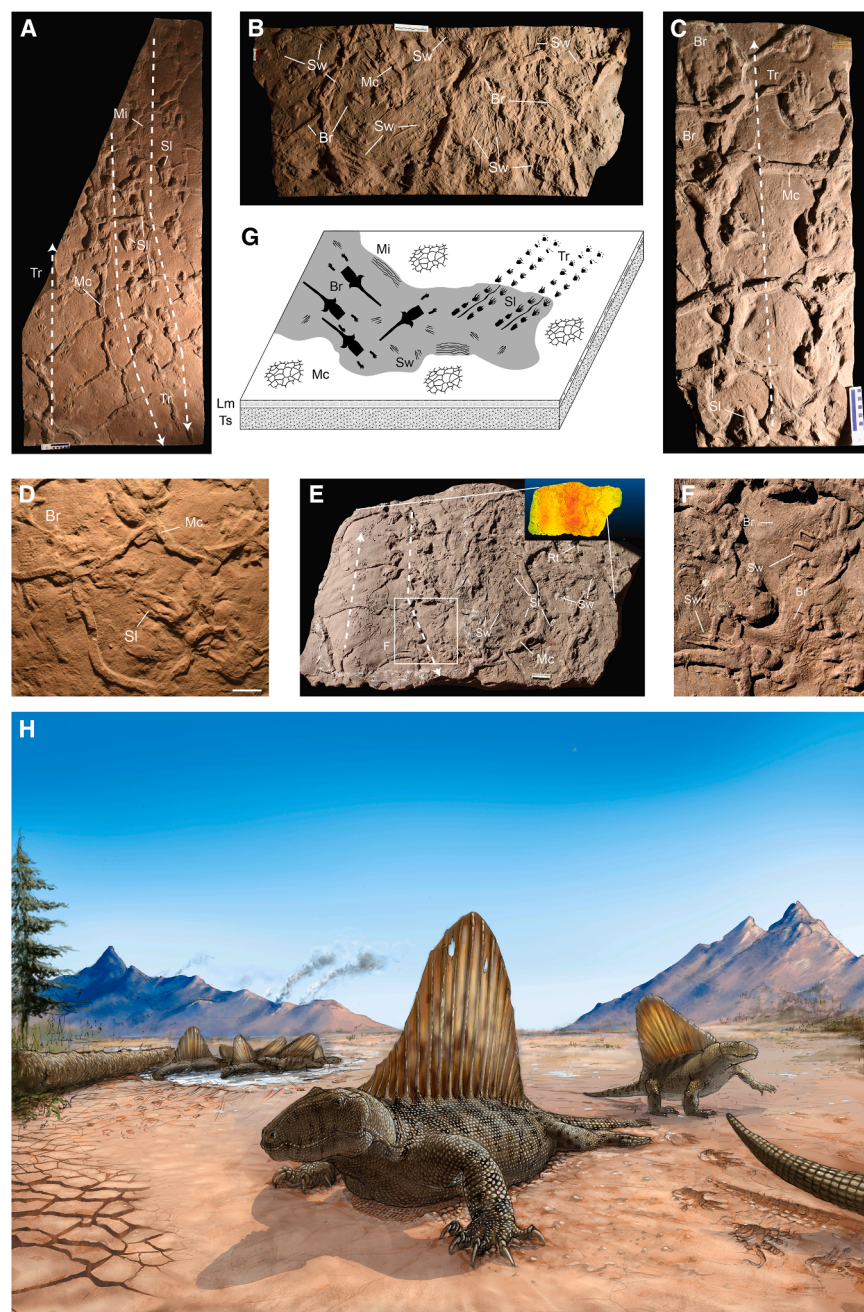


Figure 4. Paleoeology of *Bromackerichnus requiescens* n. igen. n. isp.

(A) MNG 1823. Parallel trackways of *Dimetropus leisnerianus* changing preservation along their course, associated with microbial mats and cut by mud cracks.

(B) MNG 14944. Four sphenacodontid body impressions of *Bromackerichnus requiescens* n. igen. n. isp., associated with *Dimetropus leisnerianus* trackways and swimming traces and cut by mud cracks, artificial cast.

(C) MNG 1765. Two *Bromackerichnus requiescens* n. igen. n. isp. laying side to side and a trackway of *Dimetropus leisnerianus* showing sliding traces, both cut by mud cracks.

(D) MNG 1822. *Bromackerichnus requiescens* n. igen. n. isp. and *Dimetropus leisnerianus* trackway with sliding traces, cut by mud cracks.

(E and F) MNG 13490. *Bromackerichnus requiescens* n. igen. n. isp. and indeterminate body impressions associated with swimming traces and trackways of *Dimetropus leisnerianus*, *Ichthyosaurus sphaerodactylum*, and *Varanopus microdactylus*. The trace fossils are cut by mud cracks. Note in the false color depth map from photogrammetric 3D model, in the upper right corner of (E), that the deepest areas in red are those with swimming, sliding, and resting traces.

(G) Paleoenvironmental reconstruction from the combined information of (A)–(E). Note the transition from indistinct footprints with sliding traces to well-preserved footprints in the water-to-land transition, as observed in (A). Br, *Bromackerichnus requiescens* n. igen. n. isp.; Rt, indeterminate resting trace; Sw, sphenacodontid swimming traces; Sl, sliding traces; Tr, sphenacodontid trackways; Mi, microbially induced sedimentary structures (MISS); Mc, mud cracks; Lm, thin laminated mudstone; Ts, tabular fine- to medium-grained sandstone. Arrows indicate the direction of the main trackways. All specimens in convex hyporelief; scale bars, 5 cm.

(H) Group of *Dimetrodon teutonius* resting in a pool. Notice the resting traces, the swimming traces, and the trackways indicating walking out of water. The head scales are hypothetical—they are not present in the studied specimens. Paleoart by Charlene Letenneur.

See also Table S3.

- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

L.M. ideated the study, studied the material, made measurements, analyzed data, wrote the manuscript, and made figures and tables. A.L. and M.B. studied the material, analyzed data, wrote the manuscript, and made figures. J.F. analyzed data and wrote the manuscript. All authors revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Trace fossil measurements	This paper	Table S1
Skeletal measurements	This paper	Table S2
Associated traces and sedimentary structures	This paper	Table S3
CT scan data	https://www.morphosource.org/	000720516
Nomenclature acts	https://zoobank.org/	urn:lsid:zoobank.org:act:3A2F6751-9DDB-42E8-812B-52D705F9E83D
Software and algorithms		
Agisoft Metashape Professional	https://www.agisoft.com/	N/A
Cloud Compare	https://www.danielgm.net/cc/	N/A
Paraview	https://www.paraview.org/	N/A
Amira ZIB Edition 2021.09	https://www.thermofisher.com/ie/en/home/electron-microscopy/products/software-em-3d-vis/amira-software.html	N/A
Other		
Holotype specimen of <i>Bromackerichnus requiescens</i> n. igen. n. isp.	This paper	MNG 1821
Paratype specimen of <i>Bromackerichnus requiescens</i> n. igen. n. isp.	This paper	MNG 1765
Paratype specimen of <i>Bromackerichnus requiescens</i> n. igen. n. isp.	This paper	MNG 14944

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Specimen collection

The studied material comes from the early Permian Bromacker locality in Thuringia, central Germany.⁵ This locality, near the village of Tambach-Dietharz, yielded abundant and well-preserved tetrapod footprints and trackways from sandstone quarrying activities since the late 19th century.¹⁴ These trace fossils are usually preserved as convex hyporelief at the base of sandstone layers, the “lower beds” of Eberth et al.⁵ From the 80ies of the 20th century, abundant, well-preserved and articulated tetrapod skeletons have been found from a different lithofacies, fine-grained sandstones and siltstones, the “upper beds” of Eberth et al.⁵ The studied material comes from the “lower beds” of Eberth et al.⁵ and was collected between 1895-1899 in the Seeberger Fahrt quarry (MNG 1765-1987) and after 2000 in the commercial quarry (MNG 13490-14944) of the Bromacker locality.

METHOD DETAILS

Biostratigraphy

All the material from the Bromacker locality (Figure S1) belongs to the Tambach Sandstone Member of the Tambach Formation, lately considered of Sakmarian age, based on biostratigraphy and radiometric ages of the underlying formations.³⁹ The paleoenvironment has been interpreted as an inland fluvial setting in a seasonal tropical climate.⁵

3D model generation

We obtained 3D models of the specimens through digital photogrammetry with the software Agisoft Metashape Professional. Contour lines and colour depth maps were obtained by employing the software Cloud Compare and Paraview. We analyzed the cross-section of scales of different body parts of *Bromackerichnus* n. igen. on 3D models.²⁹

The CT scan was done at the Museum für Naturkunde Berlin, Germany with a YXLON FF35 CT scanner. The segmentation of the CT scans of skeletons was done with the software Amira ZIB Edition 2021.09.

Taphonomy

Preservation of skin is rare in early amniote body fossils and hypotheses about the early evolution of epidermal appendages including scales are commonly based on molecular, morphological, microstructural and developmental studies of extant tetrapods and phylogenetic bracketing.⁴⁰ We analyzed taphonomic processes and modern-day reptile epidermal scales for comparison (Figures S2 and S3), and we found that the late Paleozoic trace fossils that include details of the skin surfaces are somewhat more extensive and span a larger phylogenetic range than the body fossils. So, we argue that it is possible to identify patterns in the evolution of epidermal scales in early amniotes through an integration of the body fossil and trace fossil records of Paleozoic tetrapod skin in a pre-existing phylogenetic framework (Figure 3). The taphonomy of skin impressions has been carefully evaluated, excluding skin-like sedimentary structures such as interference ripples and microbially-induced sedimentary structures (Figure S4). The attribution of skin structures to epidermal scales is based on morphological comparison with modern-day reptile epidermal scales (Figure S2).

Systematics

Body impressions are rarely reported from fossil vertebrates and, if present, are often not considered ichnotaxonically, with few exceptions.^{9,10} We argue that the ichnotaxonomy of such traces is, however, important for paleobiological inferences (Figure S5) and should be based on morphology and consider features that can be related to likely tracemakers. After evaluating the taphonomy of the trace fossils, only the best-preserved and most complete specimens were considered for systematics.¹¹ The proposed ichnotaxonomy is based on a differential diagnosis with morphologically similar resting trace ichnotaxa.

Nomenclatural acts

The nomenclatural acts performed in this work have been registered in ZooBank. The Life Science Identifiers (LSID) for this publication are: urn:lsid:zoobank.org:act:3A2F6751-9DDB-42E8-812B-52D705F9E83D

QUANTIFICATION AND STATISTICAL ANALYSIS

Skeletal and trace fossil measurements

Body impression, footprint and trackway measurements were listed in Table S1, Part of the footprint and trackway measurements are from Voigt⁴¹. Skeletal measurements were listed in Table S2.